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# Notes on carnivore fossils from the Pliocene Udunga fauna, Transbaikal area, Russia

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## Abstract

We provide notes of carnivore fossils from the middle Pliocene Udunga fauna, Transbaikal area, Russia. The fossil carnivore assemblage consists of more than 200 specimens including eleven genera. *Ursus*, *Parailurus*, *Parameles*, and *Ferinestrix* are representative of the animals of thermophilic forest biotopes. On the other hand, *Chasmaporthetes* and *Pliocrocuta* are probably specialized in open environment. The prosperity both in foresal and semiarid carnivores indicate that the Udunga fauna is comprised of mosaic elements.

## Introduction

The fauna dating back to the Pliocene in Udunga, Transbaikalia, Russia, comprises eleven species of mammals, such as rodents, lagomorphs, carnivores, perissodactyls, artiodactyls, and elephants (Kalmykov, 1989, 1992, 2003; Kalmykov and Maschenko, 1992, 1995 Vislobokova *et al*., 1993, 1995;; Erbajeva *et al*., 2003). The Udunga site is located on the left bank of the Temnik River, the tributary of the Selenga River in the vicinity of Udunga village (Figure 1). This mammal fauna is discovered from the red clayey beds of the Upper Neogene Chikoi Formation (Kalmykov, 1989; Erbajeva *et al*., 2003).

The fossil materials of the Pliocene Transbaikalian carnivores have been studied by many workers (e.g. Kalmykov, 1989, 1992, 2003; Sotnikova and Kalmykov, 1991; Vislobokova *et al*., 2001; Sotnikova, 2006, 2008), and these series are their ongoing research. Their works show the rich diversity of carnivores in the Pliocene Transbaikalian area and the richness is particular feature of the Udunga fauna. In this study, we remark eleven genera of carnivores from the Udunga locality, which have been recognized from the materials stored in the Southern Scientific Center (SSC), Rostov-on-Don, Russia. The preliminary study of carnivorous mammals of Udunga fauna was reported by Sotnikova and Kalmykov (1991),

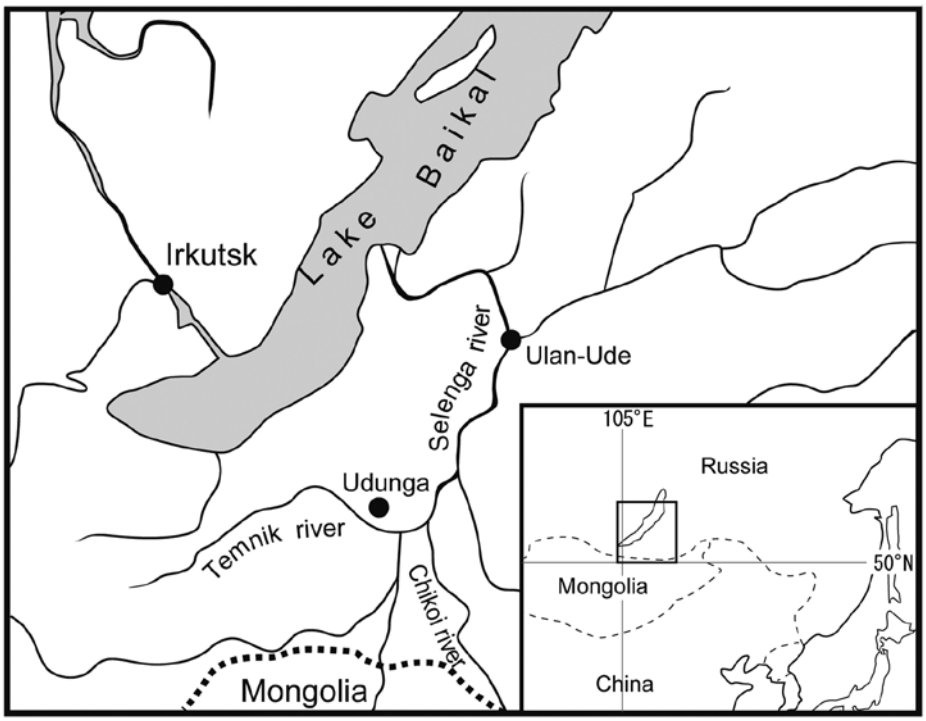


**Figure 1.** The location of the Transbaikal area. Modified from Kalmykov (2002).

but Canis sp., Gulo minor are not stored in SSC collection. The recognized species in this study are listed in Table 1.

## Remarks

### Order Carnivora Bowdich, 1821
### Family Canidae Gray, 1821
### Genus *Nyctereutes* Temmnick, 1838
### *Nyctereutes* sp. indet.

Sotnikova and Kalmykov (1991) reported the occurrence of *Nyctereutes* from the Udunga fauna. Three hemimaxillae, four hemimandibles, isolated $M^2$, and three of isolated $M_1$ of *Nyctereutes* are distinguished from the SSC collection (Table 2). There are a few *Nyctereutes* materials known in the Udunga fauna, which is identified as *Nyctereutes* sp. (Sotnikova and Kalmykov, 1991; Kalmykov, 1992, 1999, 2003; Erbajeva *et al*., 2003; Kalmykov, Maschenko, 2005, 2006; Kalmykov *et al*., 2005; Maschenko *et al*., 2007). The oldest representative of the genus *Nyctereutes* (*N*. aff. *donnezani*) is known from late Turolian Venta del Moro (Spain), so the origin is considered to appear in western part of Palaearctic region (Morales and, Aquirre, 1976). In Ruscinian, they were widespread in Europe (Alcalá and Montoya, 1989-1990; Tedford, 1995). Early representatives of *Nyctereutes* (*N. donnezani*) are known from La Gloria 4 (MN 14), La Calera (MN 15a), Layna (MN 15b),

**Table 1.** List of carnivore fossils of the Udunga fauna stored in SSC collection.

| taxon | number of specimens | references |
|---|---|---|
| *Nyctereutes* sp. indet | 11 | Sotnikova and Kalmykov (1991) |
| *Canis* sp. indet. | 2 | Sotnikova and Kalmykov (1991) |
| *Ursus minimus* | 8 | Sotnikova and Kalmykov (1991) |
| *Pannonictis* sp. indet. | 8 | Vislobokova et al (2001) |
| *Parameles suillus* | 5 | Kalmykov (1989) |
| *Ferinestrix* sp. indet. | 107 | Sotnikova (2006) |
| *Parailurus baikalicus* | 3 | Sotnikova (2008) |
| *Pliocrocuta pyrenaica* | 30 | Kalmykov (1989) |
| *Chasmaporthetes lunensis* | 4 | Vislobokova et al (2001) |
| *Lynx shansius* | 28 | Kalmykov (1989) |
| *Homotherium* sp. indet. | 2 | Kalmykov (1989) |

**Table 2.** Specimens of *Nyctereutes* sp. indet.

| Udg- | side | Material |
|---|---|---|
| 43 | R | maxilla with $M^1$ |
| 48 | R | mandible with $M_1$-$M_3$ |
| 49 | L | mandible with $P_4$ and $M_1$ |
| 50 | R | maxilla with $P^4$-$M^2$ |
| 119 | R | mandible with lower canine, $P_2$, $P_4$ |
| 161 | R | maxilla with $P_3$ and $P_4$ |
| 162 | R | $M_1$ (bloken) |
| 163 | L | $M_1$ |
| 190 | L | $M^2$ |
| ## | R | mandible with $M_1$ |
| ## | R | $M_1$ |

**Table 3.** Specimens of *Canis* sp. indet.

| Udg- | side | Material |
|---|---|---|
| 176 | L | mandible with $M_2$ |
| 2471 | | upper and lower dentitions |

Spain. Later form, *N. megamastoides* is from Villarroya (MN 16a ), El Rincon (MN 16b), La Puebla del Valverde (MN 17a), Spain (Alcalá and Montoya, 1989-1990). *Nyctereutes* is also known from the western Transbaikal area (Sotnikova and Kalmykov, 1991, Kalmykov, 1992) and China (Tedford, Qiu, 1991; Tong *et al*., 1995; Li *et al*., 2003) in Villafranchian. In Central to East Asia, *N.* cf. *sinensis* is known from western Transbaikalia (Beregovaya), and *N. megamastoides* is known from the northern Mongolia (Shamar) (Sotnikova, 1976). Tedford and Qui (1991) hypothesized that the early Pliocene Chinese and European *Nyctereutes* should be organized in the same taxon. *N. megamastoides* diverged from *N. donnezani* at the late Pliocene in Europe (Soria and Aguirre, 1976), which is morphologically comparable with *N. sinensis*. On the other hand, *N. tingi,* which is known from East Asia and suddenly occurred in the early Pliocene, is closely related to extant *N. sinensis* (Tedford and Qui, 1991). Thus, identification of *Nyctereutes* from the Udunga fauna would be important for understanding relationship between European and Asian taxon in Pliocene.

## Genus *Canis* Linnaeus, 1758

### *Canis* sp. indet.

Only two specimens of large canid are available in the SSC Udunga collection (Table 3). Left mandible with $M_2$ (Udg-0176) and isolated upper and lower dentitions (Udg-2471)

**Table 4.** Specimens of *Ursus* sp. indet.

| Udg- | side | Material |
|---|---|---|
| 16 | R | lower canine |
| 53 | L | $M_2$ |
| 54 | R | $M_2$ |
| 140 | L | maxilla with $P^4$ |
| 2001 | | upper canine |
| 2002 | L | $M_1$ |
| 2003 | R | $M_2$ |
| 2004 | R | $M_3$ |

**Table 5.** Specimens of *Pannonictis* sp. indet.

| Udg- | side | Material |
|---|---|---|
| 128 | L | maxilla with $P^4$ |
| 129 | R | maxilla with $P^3$ and $P^4$ |
| 144 | R | $P^4$ |
| 145 | R | $M^1$ |
| 150 | L | $P^4$ |
| 2400 | R | upper canine |
| 2410 | L | upper canine |
| 2400 | L | lower canine |

are obviously larger than *Nyctereutes*. These specimens are considered *Canis* but there are some small forms. *Canis* appeared in Eurasia in the middle Turolian (Mein, 1990), but their adaptive radiation occurred in Ruscinian (Vangengeim *et al*., 1998). Its oldest representatives are known from Europe such as Los Mansuetos, Concud (*C. cipio*, MN 12), Perpignan (*C. michauxi, C. adoxus*, MN 15), La Calera (*C. indetermonado*, MN 15a), Odessa catacombs (*C. petenyi*, MN 15), Villarroya (*C. indetermonado*, MN 16a), Kuruksai (*C. kuruksaensis*, *C.* ex gr. *lepophagus*, MN 16b), Kvabebi (*Canis* sp., MN 16), Etouaires (*C. etruscus*, MN 16b) (Vekua, 1972; Vangengeim *et al*., 1988; Alcalá and Montoya, 1989-1990; Mein, 1990). In China, *Canis* appeared in the late Ruscinian (Tedford, 1995; Tedford, Qiu, 1996).

## Family Ursidae Fisher de Waldheim, 1817
## Genus *Ursus* Linnaeus, 1758
## *Ursus minimus* Devèze et Bouillet, 1827 (Stuart, 1982)

Sotnikova and Kalmykov (1991), Kalmykov (1992) reported *Ursus* ex gr. *ruscinensis-minimus* from the Udunga fauna. Seven isolated teeth including upper canine, lower canine, $M_1$, $M_2$, $M_3$, and a left maxilla with $P^4$, are stored in the SSC Udunga collection (Table 4). *U. minimus* retains primitive morphological characteristics, which is closely related to the late Ruscinian or the earliest Villafranchian ursid forms (Sotnikova and Kalmykov, 1991; Kalmykov, 1992; Sotnikova, 2006). *U. minimus* Deveze et Debouillet (sin. *U. arvernensis* Croizet et Jobert) is known from three locality, such as Gaville (Val de'Arno, Italy), Puy de Dôme (France) and Layna (Spain) (Torres, 1988).

The identification of the Pliocene Russian ursid is disputed (Vekua, 1972; Sotnikova and Kalmykov, 1991; Kalmykov, 1992; Vislobokova *et al*., 1993; and Sotnikova, 2006). In Europe *Ursus* is known from the late Ruscinian localities, such as Layna (*U. ruscinensis*), Odessa catacombs (*U. arvernensis*), Weze (*U. wenzensis*) (Kowalski, 1990; Mein, 1990; Perez, Soria, 1989-1990; Vangengeim *et al*., 1998). In China *Ursus* sp. is known from Ertemte (*Ursus* sp.). The stratigraphical range of genus *Ursus* is from the late Turolian to the present.

## Family Mustelidae Fischer de Waldheim, 1817

**Table 6.** Specimens of *Parameles* sp. indet.

| Udg- | side | Material |
|---|---|---|
| 2 | L | mandible with lower canine-$M_2$ |
| 3 | L | mandible with lower canine-$M_2$ |
| 177 | L | mandible with lower canine, $P_4$, $M_1$ |
| 178 | L | mandible with $M_1$ and $M_2$ |
| 2420 | | upper canine |

## Subfamily Galictinae Reig, 1957
## Genus *Pannonictis* Kormos, 1931
## *Pannonictis* sp. indet.

Vislobokova *et al*. (2001) reported the occurrence of large galictine mustelid, *Pannonictis*, from Asian part of former USSR (Table 5). Eight of mustelid specimens including six isolated tooth, left maxilla with $P^4$, and right maxilla with $P^3$ and $P^4$, considered to be *Pannonictis*. *Pannonictis* differs from other Mustelidae in the sizes and shape of $M_1$ and $P^4$, skull, and mandible. It is close to the South American extant genus *Grison* and to the extinct genus *Enhydrictis* from the Plio-Pleistocene of Europe (Sotnikova, 1980). The Middle Pleistocene East Asian *Oriensictis* is also close to *Pannonictis* (Ogino and Otsuka, 2008). The origin of *Pannonictis* is probably in Asia. Zdansky (1927) has described a large specimen of Mustelidae gen. et sp. indet. from the accumulations of late Miocene of China, which was similar to *Pannonictis*. Sotnikova (1980) considered that both of *Pannonictis* from the northern Mongolia (Shamar, MN 16a) and China (Gaotege, MN 15) are relatives of the Zdansky' s mustelid. In Europe the oldest *Pannonictis* is known from the late Ruscinian of Hungary (Csarnota 1, MN 15) (García and Howell, 2008).

## Subfamily Melinae Burmeister, 1850
## Genus *Parameles* Rostshin, 1949
## *Parameles suillus* (Teilhard et Leroy) 1945

Kalmykov (1989) reported the occurrence of *Parameles suillus* from the Udunga fauna. Four left mandibles and isolated upper canine are considered to be *Parameles suillus* in the SSC Udunga collection (Table 6). Left mandible (Udg-0003) is described by Kalmykov (2003: p. 31, Fig.4). *P. suillus* (= *Meles suiilus*), which has been described from adjournment of the sediments of Yushe (Teilhard de Chardin and Leroy, 1945), was found from Shamar (northern Mongolia) (Sotnikova, 1980). Several melid fossils have already been described under the different names from the early Pliocene Europe: *Parameles* from Odessa catacombs (Ukraine) and Weze (Poland) (Stach, 1951). According to Sotnikova and Kalmykov (1991), the priority belongs to *Parameles* Rostchin, so *Parameles* should include "*Meles*" *genevauxi* from Montopoli (France), *Arctomeles pliocaenicus* from Weze (Poland), *Parameles ferus* from the Odessa catacombs (Ukraine), *Meles suillus* from Yushe, Ertemte (China), Shamar (North

**Table 7.** Specimens of *Ferinestrix* sp. indet.

| Udg- | side | Material |
|---|---|---|
| 4 | R | mandible with $M_1$ |
| 6 | L | mandible with $P_3$ , $P_4$, and $M_2$ |
| 7 | L | mandible with lower canine-$M_2$ |
| 8 | L | mandible with $P_3$ -$M_1$ |
| 9 | R | mandible with $P_3$ -$M_1$ |
| 10 | L | mandible with $I_2$, lower canine-$M_1$ |
| 11 | L | mandible with $P_3$ |
| 12 | R | mandible with $P_3$ |
| 13 | L | mandible with lower canine-$M_2$ |
| 14 | L | mandible with $P_4$ and $M_1$ |
| 18 | L | mandible with $P_2$ and $P_4$ |
| 19 | L | maxilla with $P^4$ |
| 20 | L | mandible with $P_4$-$M_1$ |
| 31 | L | mandible with $P_3$-$M_1$ |
| 32 | L | mandible with m2 |
| 46 | L | mandible with $P_4$-$M_2$ |
| 47 | R | mandible with lower canine-$M_2$ |
| 55 | L | $M_1$ |
| 56 | R | $M_1$ |
| 57 | | lower canine |
| 68 | L | $M_1$ |
| 69 | L | maxilla with $P^3$ and $P^4$ |
| 70 | L | $M^1$ |
| 72 | L | mandible with lower canine-$M_1$ |
| 73 | L | mandible with lower canine-$M_2$ |
| 74 | L | mandible with $M_1$ and $M_2$ |
| 75 | R | maxilla with $P^4$ and $M^1$ |
| 79 | L | maxilla with $P^4$ and $M^1$ |
| 82 | L | mandible with $P_4$ and $M_1$ |
| 83 | L | maxilla with $P^4$ and $M^1$ |
| 89 | R | mandible with lower canine-$M_1$ |
| 90 | L | $M^1$ |
| 91 | R | mandible with $P_4$ and $M_1$ |
| 111 | R | mandible with $M_1$ |
| 113 | R | mandible with $P_4$ and $M_1$ |
| 114 | L | mandible with $M_1$ |
| 115 | L | mandible with $M_1$ |
| 116 | L | mandible with $P_3$-$M_1$ |
| 117 | L | mandible with $P_3$-$M_1$ |
| 122 | R | $M^1$ |
| 123 | L | maxilla with $P^3$ and $P^4$ |
| 124 | R | $P^4$ |
| 125 | R | $M^1$ |
| 130 | R | maxilla with $P^3$ |
| 132 | R | mandible with $P_3$ -$M_1$ |
| 133 | R | mandible with lower canine, $P_3$, $P_4$ |
| 135 | R | maxilla with $P^4$ and $M^1$ |
| 136 | L | $M^1$ |
| 137 | L | maxilla with $P^4$ and $M^1$ |
| 141 | L | maxilla with $P^4$ |
| 158 | R | maxilla with $P^3$ and $P^4$ |
| 159 | L | maxilla with $P^3$ - $M^1$ |
| 164 | L | maxilla with $M^1$ |
| 165 | R | maxilla with $P^4$ and $M^1$ |
| 167 | R | mandible with lower canine and $P_2$ |
| 168 | R | mandible with $M_1$ |
| 169 | | upper incisor |
| 170 | L | mandible with $P_2$ -$M_1$ |
| 171 | R | mandible with $P_3$-$M_2$ |
| 172 | L | mandible with $P_4$-$M_2$ |
| 173 | L | mandible with lower canine-$M_1$ |
| 174 | R | mandible with $P_2$ -$M_1$ |
| 175 | R | maxilla with $P^3$-$M^1$ |
| 185 | L | mandible with lower canine-$M_1$ |
| 1297 | R | mandible with $P_4$ and $M_1$ |
| 1302 | L | upper canine |
| 1303 | R | $M^1$ |
| 1304 | L | $P^3$ |
| 2005 | R | lower canine |
| 2006 | L | maxilla with $P^3$ and $P^4$ |
| 2007 | L | mandible with $M_1$ |
| 2009 | R | upper canine |
| 2010 | L | upper canine |
| 2011 | R | $M^1$ |
| 2012 | R | $M_2$ |
| 2013 | L | $M_2$ |
| 2016 | R | maxilla with $M^1$ |
| 2017 | R | maxilla with $P^4$ and $M^1$ |
| 2018 | L | maxilla with $M^1$ |
| 2031 | R | mandible |
| 2005 | L | lower canine |
| 2016 | L | $M^1$ |
| 2017 | R | $M^1$ |
| 2348 | | upper canine |
| 2349 | | upper canine |
| 2352 | | upper canine |
| 2353 | | upper canine |
| 2459 | | upper canine |
| 2369 | | upper canine |
| 2370 | | upper canine |
| 2410 | | lower canine |
| 2411 | | lower canine |
| 2412 | | lower canine |
| 2413 | | lower canine |
| 2415 | | upper canine |
| 2416 | | upper canine |
| 2439 | | upper canine |
| 2431 | | upper canine |
| 2428 | | upper canine |
| 2429 | | upper canine |
| 2424 | | lower canine |
| 2425 | | lower canine |
| 2426 | | lower canine |
| 2454 | | lower canine |
| 2455 | | lower canine |
| 2472 | | upper canine |
| 2408 | R | $M_1$ |

Mongolia) and Udunga. Thus, the stratigraphical range of *P. suillus* is considered from the end of Turolian (MN 13) to the beginning of early Villafranchian (MN 16a) (Li *et al*., 1984; Wolsan, 1989; Sotnikova, Kalmykov, 1991; Kalmykov, 1992; Tedford, 1995; Vangengeim *et al*., 1998).

**Table 8.** Specimens of *Parailurus baikalicus*.

| Udg- | side | Material |
|---|---|---|
| 1 | R | mandible with lower canine-$M_2$ |
| 51 | R | $M_2$ |
| 52 | R | $M_1$ |

## Genus *Ferinestrix* Bjork, 1970
## *Ferinestrix* sp. indet.

An enigmatic form of large badger is identified as *Ferinestrix* sp. by Sotnikova (2006). Formerly a large badger was defined as Mustelidae gen. nov. et sp. nov (Kalmykov, 1989). The most abundant carnivore in the SSC Udunga collection is *Ferinestrix* (Table 7), which was only known from the Pliocene North American Hagerman local fauna and established on the basis of the fragment of mandible with incomplete $M_1$ (Bjork, 1970).

## Family Ailuridae Gray, 1843
## Genus *Parailurus* Schlosser, 1899
## *Parailurus baikalicus* Sotnikova, 2008

Only thee specimens are available to us (Table 8). Right mandible with complete cheek teeth row (Udg-0001) has been reported by Kalmykov (2002: p. 211, Fig. 3). All dentition of Udg-0001 are considerably worn,indicating that it belong to an old individual, while two isolated teeth, right $M_1$ (Udg-0052) and $M_2$ (Udg-0051), have weak dental attrition.

These ailurid specimens are considered to belong to the large lesser panda, *Parailurus baikalicus* Sotnikova, 2008 from Udunga. Although extant lesser panda, *Ailurus flugens* is limited to the Himalayan highland forest, the extinct large lesser panda *Parailurus* is widely distributed in the Pliocene northern hemisphere including Europe, Asia, and North America (Kundrát, 1997; Morlo and Kundrát, 2001; Sasagawa *et a*l., 2003; Wallace and Wang, 2004; Sotnikova, 2008). Several specimens of Ailuridae are known from the Udunga fauna and numerous lists of fauna was specified as *Ailurus* sp. (Kalmykov, 1999, 2003, Erbajeva *et al*., 2003; Kalmykov, Maschenko, 2005, 2006; Kalmykov *et al*., 2005; Maschenko *et al*., 2007). Erbajeva *et al*. (2003) identified these specimens to *Parailurus* sp., but later it was redescribed *as Parailurus baikalicus* (Sotnikova, 2008) on the basis of the fragment left maxilla (No. 962/58, БФ ГИН) with $P^4$, $M^{1-2}$ and the alveolus of the distal root of $P^3$. The Transbaikalian *P. baikalicus* is larger than the European *P. anglicus,* but likely corresponds to *P. hungaricus*. *Parailurus* sp. from the Pliocene Japan (Sasagawa *et al*., 2003) differs from *P. baikalicus* by having primitive characteristics on $P^4$.

**Table 9.** Specimens of *Pliocrocuta* sp. indet.

| Udg- | side | Material | Udg- | side | Material |
|---|---|---|---|---|---|
| 24 | R | mandible with $P_2$-$M_1$ | 187 | L | maxilla with $P^3$ and $P^4$ |
| 25 | R | mandible with lower canine, $P_4$, $M_1$ | 188 | L | maxilla with $P^2$-$P^4$ |
| 26 | R | mandible with lower canine-$M_1$ | 1301 | L | $I_1$-$I_3$ |
| 27 | L | mandible with $P_2$-$M_1$ | 2008 | L | $P^3$ |
| 29 | R | mandible with lower canine-$M_1$ | 2014 | R | $M_1$ |
| 30 | L | mandible with $M_1$ | 2015 | R | mandible |
| 41 | R | mandible with $P_2$-$M_1$ | 2019 | R | mandible |
| 71 | R | mandible with lower canine-$M_1$ | 2020 | | lower incisor |
| 100 | L | $P^4$ | 2021 | R | $I_3$ |
| 156 | R | mandible with $P_3$ and $P_4$ | 2022 | L | $I_3$ |
| 180 | R | mandible with $P_2$-$M_1$ | 2028 | R | mandible with $P_3$-$M_1$ |
| 181 | R | mandible with $P_3$-$M_1$ | 2032 | R | $M_1$ |
| 182 | L | mandible with lower canine-$M_1$ | 2033 | L | $P_3$ |
| 183 | R | mandible with lower canine-$M_1$ | 2034 | L | $P_4$ |
| 186 | R | maxilla with $P^3$ and $P^4$ | 2035 | L | $M_1$ |

## Family Hyaenidae Gray, 1869
## Genus *Pliocrocuta* Koretzoi, 1938
## *Pliocrocuta pyrenaica* (Deperet), 1890

30 specimens are considered to be *Pliocrocuta pyrenaica* (Table 9). Right mandible (Udg-0026) of *P. pyrenaica* has been reported by Kalmykov (2003: p. 32, Fig.5). *P. pyrenaica* retains primitive morphological feature and similar to the late Ruscinian or the earliest Villafranchian hyaenid form (Kalmykov, 1992; Sotnikova, 2006). The identification of *Pliocrocuta* is constructed based on tooth morphology. The characteristics of $M_1$ differs from that of *Hyaena*. The length of $P_4$ is much greater than that of *Ictitherium* (Sotnikova, 1989). *Pliocrocuta* possibly includes fossil hyenids from Layna (*Hyaena pyrenaica*), Odessa catacombs (*Crocuta* cf. *sivalensis*), Beregovaya (*Crocuta* cf. *licenti*), Kuruksai (*Pachycrocuta* cf. *perrieri*), Leijiahe (*Hyaena licenti*) (Kalmykov, personal communication). *P. pyrenaica* is common not only in Udunga but also in the early Pliocene of Europe, such as Serrat den Vocquer (France), Layna (Spain), and Odessa catacombs (Ukraine). *Pliocrocuta* is distributed in the wide area of northern Eurasian continent from Spain to the Baikal lake in the early Pliocene (Vangengeim *et al*., 1998). In the Pliocene of Europe some stages of the development of the genus from *P. pyrenaica* of Ruscinian to the derived form, *P. perrieri* (Sotnikova, 1989). In Central Asia *Pliocrocuta* is known from the early to middle Pleistocene. Kurten (1956) marked finds of two large forms such as *P. brevirostris licenti* and *P. brevirostris sinensis* in Zhoukoudian, northern China. Subspecies of *P. brevirostris* is also known from Transbaikalia (Zasukhina, Tologoi) and from the Northern Mongolia (Nalaiha) (Vislobokova *et al*., 1995). *P. perrieri* is reported from the late Pliocene localities in Asia, such as Youhe (China) and Kuruksay (southern Tajikistan) (Howell, Petter, 1980; Sotnikova, 1989). In Asia, *Pachycrocuta pyrenaica orientalis* is known from the Villafranchian China (Qiu, 1987). Unfortunately, the Chinese material on hyaenid is not stratified, therefore new data on *P. pyrenaica* from the western Transbaikal area would be

**Table 10.** Specimens of *Chasmoporthetes* sp. indet.

| Udg- | side | Material |
|---|---|---|
| 45 | L | mandible with $P_2$-$M_1$ |
| 184 | L | mandible with $P_2$-$M_1$ |

**Table 11.** Specimens of *Lynx shansius*.

| Udg- | side | Material |
|---|---|---|
| 15 | R | mandible with lower canine-$M_1$ |
| 22 | R | mandible with lower canine-$M_1$ |
| 33 | L | mandible with lower canine, $P_4$, $M_1$ |
| 34 | R | mandible with lower canine, $P_4$, $M_1$ |
| 35 | R | mandible with lower canine-$M_1$ |
| 36 | R | mandible with lower canine-$M_1$ |
| 38 | R | mandible with $P_3$-$M_1$ |
| 39 | L | mandible with $P_3$-$M_1$ |
| 40 | L | mandible with lower canine-$M_1$ |
| 44 | L | mandible with $P_3$-$M_1$ |
| 77 | R | maxilla with $P^3$ and $P^4$ |
| 86 | R | mandible with lower canine-$M_1$ |
| 110 | R | mandible with $P_3$-$M_1$ |
| 118 | L | mandible with $P_3$ and $P_4$ |
| 127 | R | maxilla with $P^3$ and $P^4$ |
| 134 | R | mandible with $P_3$ and $P_4$ |
| 138 | L | mandible with lower canine, $P_3$, $P_4$ |
| 139 | R | mandible with $P_4$ and $M_1$ |
| 157 | L | mandible with $I_3$ and $P_3$ |
| 160 | R | mandible with lower canine-$M_1$ |
| 166 | L | maxilla with $P^4$ and $M^1$ |
| 179 | L | mandible with lower canine-$P_4$ |
| 1295 | L | mandible with $P_3$-$M_1$ |
| 1305 | | lower canine |
| 1306 | | lower canine |
| 1307 | | lower canine |
| 1308 | R | mandible with lower canine and $P_3$ |
| 1309 | R | $P_4$ |

important for the study of its dispersal and evolution.

## Genus *Chasmaporthetes* Hay, 1921

### *Chasmaporthetes* sp. indet.

Vislobokova *et al*. (2001) reported the occurrence of a gracile hunting hyaena, *Chasmaporthetes*, from Asian part of the former USSR. Only two left mandibles with $P_2$-$M_1$ considered to be this genus (Table 10). *Chasmaporthetes* was widely distributed in the Plio-Pleistocene northern hemisphere including North Africa, Europe, Asia, and North America (e.g. Hay, 1921). In Asia *Chasmaporthetes* (*C. lunensis*) is discovered from the late Pliocene of the Northern Mongolia (Shamar) and Udunga. The fossil specimens of the hunting hyaena are discovered in western Transbaikal area (Beregovaya) and Tajikistan (Kuruksay), and have been described as *Euryboas* (Sotnikova, 1974, 1976, Vangengeim *et al*., 1988). Repenning (1967) has proposed an assumption that *Euryboas* is a synonym of genus *Chasmaporthetes*. Savage and Curtis (1970) and Kurtén and Werdelin (1988) supported his opinion. However, the priority of the genus *Chasmaporthetes* has been restored even later (Kurten and Crusafont, 1977). According to Sotnikova (1994), *Chasmaporhtetes* includes *C. borissiaki* (presumably late Miocene, Moldova), *C. exitelus* (late Miocene, China), *C. lunensis* (Pliocene - early Pleistocene, Eurasia), *C. ossifragus* (late Pliocene - early Pleistocene, North America), *C. nitidula* (late Pliocene - early Pleistocene, Africa). Thus, chronological distribution of *Chasmaporthetes* is from the late Miocene to the early Pleistocene.

**Table 12.** Specimens of *Homotherium* sp. indet.

| Udg- | side | Material |
|---|---|---|
| 21 | R | mandible with lower canine, $P_4$, $M_1$ |
| 23 | R | mandible with $P_4$ and $M_1$ |
| 76 | R | $P^4$ |
| 101 | R | $P^4$ |

## Family Felidae Gray, 1821
## Genus *Lynx* Kerr, 1792
## *Lynx shansius* Teilhard et Leroy, 1945

Kalmykov (1989) reported the occurrence of *Lynx shansius* from the Udunga locality. 28 specimens are considered to be this species in the SSC Udunga collection (Table 11) and a right mandible (Udg-0160) has been described by Kalmykov (2003: p. 34, Fig. 6). *Lynx* from Udunga is known to be one of the oldest lynxes: its morphology is more primitive than that of *Lynx shansius* from the Shamar and Yushe and *L. issiodorensis* from Pardines (France) and Val d'Arno (Italy) (Kurten and Werdelin, 1984). *Lynx* appeared in the late Ruscinian and is known from Moldova and Odessa catacombs (Vangengeim *et al*., 1998).

## Genus *Homotherium* Fabrini, 1890
## *Homotherium* sp. indet.

Kalmykov (1989) firstly reported the occurrence of *Homotherium* sp. from the Udunga locality. Two right mandibles and two isolated right $P^4$ are considered to be *Homotherium* in the SSC Udunga collection (Table 12). *Homotherium* is considered to have separated from *Machairodus* at the end Miocene (Anton and Galobart, 1999), but *H. crenatidens* is known from the Villafranchian of Eurasia (Bajgusheva, 2000; Hemmer, 2001; Sotnikova *et al*., 2002). The saber-toothed cat, Machairodontinae, is discovered from the Ruscinian locality of Europe and Asia, but the materials are so fragmentary to define their essential characteristics (Vekua, 1972; Perez, Soria, 1989-1990). *Homotheriun* sp. from the Ruscinian Odessa catacombs (Ukraine), differs from the Villafranchian specimen in its primitive characteristics (Vangengeim *et al*., 1998).

## Discussion

Eleven genera of carnivores have been recognized from the SSC Udunga collection (Table 1). The Udunga fauna is recognized as the end of early Pliocene (Kalmykov, 1989, 1992, 2003; Sotnikova and Kalmykov, 1991; Kalmykov and Malaeva, 1994; Kalmykov and Maschenko, 2005, 2006; Kalmykov *et al*., 2005; Maschenko *et al*., 2007; Maschenko *et al*., 2007) or the early Late Pliocene (MN 16a, Vislobokova *et al*., 1993; Vislobokova *et al*., 1995; Erbajeva *et al*., 2003) on the basis of biostratigraphical study of many kind of mammals.

However, the Pliocene Eurasian carnivores were widely distributed spaciotemporally, and carnivore taxa of the Udunga fauna have close relationships not only to the Eurasian but also to the African and North American assemblages.

Vislobokova *et al.* (1995) referred that the occurrence of *Parameles suillus* and *Ursus minimus* from the Udunga fauna indicates analogues with Beregovaya assemblage (MN 16b; Transbaikal, Russia) and Shamar assemblage (2.8 Ma; Mongolia). The former carnivoran assemblage is represented by *Nyctereutes sinensis*, *Eucyon* cf. *minimus*, *Chasmaporthetes lunensis*, *Lynx shansius* and *Acinonyx* cf. *pardinensis* (Alexeeva and Erbajeva, 2006). The latter carnivoran assemblage is represented by *Nyctereutes megamostoides*, *Mustela* sp., *Pannonictis pachygnata*, *Meles* (=*Parameles*) *suillis*, *Hyaena* cf. *licenti*, *Euriboas* cf. *lunensiss*, *Felis* (=*Lynx*) *shansius*, and *Acinonyx* sp. (Sotnikova, 1980 and Zazhigin, 1989). Vislobokova *et al.* (1995) also pointed out that *Ursus minimus*, *Pachycrocuta* (=*Pliocrocut*a) *pyrenaica*, and felids are comparable to the Italian Triversa fauna (MN 16a; Azzaroli *et al.*, 1988). The Khapry faunal assemblage reported from the coastal zone of Azov Sea, Russia, (MN 17) was recently revised by Sotnikova *et al.* (2002), where the carnivoran assemblage is represented by *Nyctereutes megamostoides*, *Canis* cf. *senezensis*, *Lutra* sp., *Pannonictis nesti*, *Pliocrocuta perrieri*, *Pachycrocuta breviostris*, *Homotherium crenatidens*, *Acinonyx pardinensis*, and *Lynx issiodorensis*. Sotnikova (2008) referred that the similarity of *Pliocrocuta* and *Parameles* from the Udunga fauna to corresponding forms from the fauna of Odessa Catacombs, Ukraine (terminal Ruscinian).

Qiu and Qiu (1995) summarized the Chinese Neogene mammalian faunas and described the two Pliocene faunas from Shanxi Province. In the Yushe basin, *Pliohyaena* (=*Pliocrocuta*) *pyrenaica*, *Chasmaporthetes*, and *Nyctereutes* have been discovered from Gaozhuang fauna with a paleomagnetic age of 5.2 - 3.4 Ma. Deng *et al.* (2004) reported the Early Pliocene (MN14 - MN15) Hewangjia mammalian assemblage, Gansu Province, which includes three carnivoran genera, *Promephitis* sp., *Chasmaporthetes* sp., and *Hyaenictitherium wongi*, while *Ursus*, *Nyctereutes*, and *Canis* have not been found there. The absence of these forestal elements indicates that the sedimentary paleoenvironment of the Hewangjia fauna was dry condition.

*Ursus*, *Parameles*, and *Pliocrocuta* of the Udunga fauna show primitive features (Sotnikova, 2006) and these taxon borrow(???) heavily from the Ruscinian form. *Chasmaporthetes*, *Parailurus*, *Gulo*, and felids are discovered across the Northern Hemisphere including Europe, Asia, North Africa, and North America. The enigmatic large badger, *Ferinestrix*, was only known from the Pliocene North American Hagerman local fauna (Bjork, 1970). As mentioned above, carnivores of the Udunga fauna are considerable to the evidence of active exchanges between the New World and Old World in the Pliocene and this fauna is important for discussing about mammalian dispersal event in the Northern Hemisphere at the period. In addition, this fact shows the difficulty to use carnivore to the biostratigraphical study.

On the other hand, feeding habitat of carnivore is clearly discriminated from the fossil materials and it is useful to reconstruct the paleoenvironment. The abundance of animals of thermophilic forest biotopes and their unusual composition (with *Ursus*, *Parailurus*, *Parameles*, and *Ferinestrix*) is peculiar feature of carnivores of the Udunga fauna (Sotnikova, 2006). However, *Hipparion* (*H. houfenese* and *H. tchicoicum*), *Dicerorhinus*, bovids, and *Chasmaporthetes* are representative of the open land elements. The occurrence of both forestal and semiarid mammals indicates that the Udunga fauna is comprised of mosaic elements.

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